DISTURBANCE, PERSISTENCE AND DIVERSITY OF

THE LONGLEAF PINE-BUNCHGRASS ECOSYSTEM[1]

by

Larry Landers and Dale Wade[2]

ABSTRACT: Understanding the factors that produce and maintain diversity and persistence of the longleaf pine-bunchgrass ecosystem are key to its conservation. We develop the hypotheses that this ecosystem is (1) persistent because a climate-site-fire-plant interaction reinforces dominance of the longleaf pine-bunchgrass ensemble; and (2) diverse because perforation of that dominance regime by disturbance-gradient-faunal impacts results in fine-grained, fluid resource mosaics. This ecosystem functions like a membrane being punctured by disturbances, yielding great diversity as patches keep opening, then giving way to pine-grass dominance. This system produces renewable resources that can be harvested, but management must be careful not to exceed the capacity of longleaf pine and bunchgrass to maintain dominance.

INTRODUCTION

The longleaf pine (Pinus palustris Mill.)-grassland (chiefly wiregrass,[Aristida stricta or A. beyrichiana] and bluestems, [Schizachyrium tenerum or S. scoparius]) system historically dominated uplands of the southern U.S. on a regional scale occupying ca. 93 million acres (Frost 1993). This ecosystem is distinguished by open pine forests, woodlands, and savannas with a grass-dominated groundcover. It is suggestive of a "biome" in that it was intricately integrated with both the regional climate and with Coastal Plain expanses and sloping terrain of adjacent provinces. This ecosystem generated fires which influenced the organization and function of ancillary neighboring plant communities, none of which were completely exempt from this natural force. It thus served as the hub of a regional complex of ecosystems.

Although prone to disturbance and devoid of fertile soils or strata of mixed species, these "pine barrens" are remarkably persistent and diverse. They have occupied the same area for thousands of years (Delcourt and Delcourt 1987; Watts 1980) and are one of the most species-rich ecosystems outside the tropics (Peet and Allard 1993). The longleaf-bunchgrass ecosystem may in fact have the most species-rich forest groundcover in the world. Understanding the factors that produce and maintain longleaf pine

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[2] J. Larry Landers (deceased), Joseph W. Jones Ecological Research Center at Ichauway, Newton GA 31770, and Dale D. Wade, USDA Forest Service, Southern Forest Fire Laboratory, Rt. 1, Box 182A, Dry Branch, GA 31020.

forest diversity and persistence are fundamental to the conservation of this ecosystem.

We hypothesize that (1) this ecosystem is persistent because a climate-site-fire-plant interaction reinforces dominance of the longleaf pine-bunchgrass ensemble and, (2) that the diverse faunal blend of specialists and opportunists that inhabit this system is contingent on expanses of fine-grained habitat mosaics with three components: a) persistent elements of a fire-pine-grass dominance regime, b) ephemeral elements resulting from perforation of this dominance regime by disturbance and gradient effects, and c) multi-species use of excavations made by key animals.

PERSISTENCE ELEMENTS

The longleaf pine region lies between the tropical and temperate zones. For several thousand years climate has been fairly consistent, particularly the long hot growing seasons and abundant rain. Thus energy does not limit productivity. This climate, however, produces a drought every 22 years or so which lasts 5 or more years (Plummer et al. 1980), plus the most frequent wind and lightning storms in North America. The region also experiences tropical storms every few decades (Neumann et al. 1981).

These factors set the stage for frequent lightning fires; fires that are promoted by key plants. Longleaf pine strongly dominates the overstory and transforms lightning strikes into fire, while bunchgrasses strongly dominate the groundcover and, with the help of pine needles spread fire throughout the community (Landers 1991). These key plants exhibit pronounced fire tolerance, are long-lived, and are efficient at gathering nutrients and water which reinforces their dominance and restricts the rate and spatial scale of vegetation change, including species turnover. In the absence of recurrent fire, shade from taller shrubs (Lewis and hart 1972) and the accumulation of strongly acidic pine needles (Hodgkins 1958) drastically limit the herbaceous flora. Thus pyrogenic selection has made longleaf pine and bunchgrasses crucial to the indefinite persistence of this community.

The number of lightning-caused fires peaks May through early August but the preponderance of acreage burned generally occurs in May. Komarek (1964) found over 90% of lightning ignitions in northern Florida took place during this 3 1/2 month period. Maintaining this seasonality is necessary for the competitive success of key species, and to the long-term perpetuation of this ecosystem. Longleaf pine is less likely to be injured, flowers of some groundcover species are more conspicuous, and other key species will only flower after fires during this period. Christensen (1977) found that fire-released nutrients were leached from the rhizosphere within four months ~~so~~ keeping nutrients available through rapid plant uptake and luxury consumption depends strongly on the season of fire occurrence (Gilliam 1988).

Site factors help promote frequent burning of this ecosystem. Quartz sands, which comprise the substrate over much of the longleaf pine range, dry quickly after precipitation. These oligotrophic sites also engender vegetation that is recalcitrant to biological decomposition because of its high C:N ratio, but is amenable to thermal decomposition. Thus chronic fire coupled with resistance of quartz sands to weathering maintain a soil structure (Heyward and Tissot 1936) and nutrient dynamics that favor residents and inhibit soil building (McKee 1982) that would promote extrinsic species. Competition from these invaders is deflected by recurrent fires. Thus a feedback loop exists that involves climate, key plants, and vast quick-drying expanses that are topographically susceptible to disturbances that all interact to maintain a chronic fire regime. This loop coupled with prolific plant growth strengthens the pine-grass dominance, which leads to a persistent ecosystem.

DIVERSITY ELEMENTS

But how can such a system support so many species on infertile sites with only two plant layers, one dominated by a single pine species and the other by a bunchgrass? We think the diversity of this ecosystem results: 1) from frequent interruption of the dominance regime by disturbance, 2) because the system spans elevation-moisture gradients along which different plants and animals specialize and, 3) because of commensalism fostered by the activities of keystone animals.

Disturbance Factors.--Most of the flatwoods probably burned every year or two, while the sandhills where edaphic factors reduce the rate of fuel accumulation, and the more dissected topography of the Piedmont, burned at least twice a decade. Chronic fire at a given location resulted from large lightning-caused fires rather than from many local ignitions per unit area. Native Americans extensively supplemented and expanded this natural growing-season fire regime utilizing the dormant season as well. They were, in turn, followed by European settlers who burned every year for the next several hundred years - in the fall to flush game from thickets and create habitat, in the winter to protect their turpentining operations, and in the spring to "freshen" forage for their livestock[3]. Humans have thus continually exerted a major impact on pyrodiversity in the southern United States, probably since soon after their arrival over 12,000 years ago (Christensen 1981). They increased pyrodiversity by expanding the burning season to all twelve months, but decreased it on some sites by shortening the fire-return interval, thereby reducing potential fire intensity. Attempts to exclude fire from this ecosystem have a stifling affect on pyrodiversity, most fires being suppressed when small, but those few that escape initial attack likely to be uncharacteristically intense and destructive.

Although ill-timed late summer and early fall fires sometimes kill longleaf pine of all ages (Boyer 1990; Chapman 1957), lightning strikes are the major source of mortality (Komarek 1968; Platt et al. 1988). Bark beetles are the second largest cause of longleaf pine mortality and usually follow lightning strikes. They are important in that they increase gap patch size. As dead trees break up, fire quickly consumes the resinous debris, but subsequent growing-season burns in these forest openings tend to be very patchy because of the lack of pine needles[4]. Wind-driven fires after the first hard frost of the dormant-season, on the other hand, tend to be more uniform in coverage.

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[3] Jim Stevenson. 1989 Instructors outline "Why we burn" in Florida Inter-agency Basic Prescribed Fire Training Course.

[4] William Michener, personal communication. Joseph W. Jones Ecological Research Center at Ichauway, Newton GA 31770

Windstorms in the form of hurricanes, tornados, and thunderstorm microbursts are also important in overstory dynamics, particularly on wet sites. The impact scale increases with the scale and intensity of wind damage. Down logs make fire dams that create temporary downwind fire shadows where pine seedling establishment is enhanced (Schwarz 1907). When they burn, adjacent groundcover is killed, soil is altered, and sites are created where micro-scale succession occurs. Although good longleaf seed crops occur infrequently, fire keeps these gaps open until colonized by longleaf pine (Platt et al.1988).

Resource Variation.--Resources such as light, water, nutrients and space, and special features such as pocket gopher digs vary along a gradient from xeric sandhills to depression ponds. Longleaf pine and bunchgrass give way to sand pine (*P. clausa* (Chapm. ex Engelm.) Vassy & Sarg.) scrub at the dry extreme and to slash (*P. elliottii* var. *elliottii*) and loblolly (*P. taeda* L.) pine at the wet end. Excellent in-depth discussions of Coastal Plain vegetative assemblages can be found in Abrahamson and Hartnett (1990), Myers (1990), Stout and Marion (1993), and Ware, Frost and Doerr (1993). Fire induces small-scale temporary changes in these resources along the elevation-moisture gradient. Complexity is added by frequent treefalls associated with lightning and beetles, and faunal excavations. Infrequent wind events and hydrologic extremes have much wider impact. These disturbances provide both ephemeral (e.g. dead wood, hardwood enclaves, bare mesic/damp patches) and more stable (e.g. old live pines, treeless spaces, swards, bare xeric patches) resource features. A broad array of habitats are thus continually available which allow opportunists to coexist with more permanent plant species. The result is an unusually diverse ground flora (Hermann 1993).

Commensalism.--Frequent fires characteristic of this ecosystem preclude litter accumulation thereby restricting microfauna that colonize duff and upper soil horizons, and severely limiting soil building processes that take place in the absence of fire. Habitat heterogeneity resulting from disturbance and resource variation do enhance faunal diversity, but in this case through commensalism in the form of multi-species use of excavations made by key animals which are favored by frequent fire.

The gopher tortoise (*Gopherus polyphemus*) is the only excavator of large, open ground burrows. These burrows are used extensively by 60 vertebrate and 302 invertebrate species (Jackson 1989), at least 17 of which are obligate. This tortoise is a seed dispersal agent of some plants and its mounds are used as regeneration sites by some plants and animals. The pocket gopher (*Geomys* spp.) is the only excavator of large, closed tunnels. These are used by numerous invertebrates, at least 16 of which are obligate. Its mounds are used as regeneration sites by some plants. The southern fox squirrel (*Sciurus niger*) is the only known excavator and dispersal agent of certain hypogenous mycorrhizae (*Elaphomyces* and others) (Weigl et al. 1989). The role of bark beetles (*Ips* and turpentine) has already been mentioned; they invade lightning-struck pines, then kill groups of surrounding pines creating gaps that become important sites for longleaf pine regeneration. Red-cockaded woodpeckers (*Picoides borealis*) are the only known excavators of cavities in living pines. These cavities are used extensively by ca. 27 other bird species as well as by flying squirrels (*Glaucomys* spp.) and broad-headed skinks (*Eumeces laticeps*).

MANAGEMENT CONSIDERATIONS

This system functions like a membrane being punctured by disturbances, yielding great diversity as patches keep opening, then giving way to longleaf pine/bunchgrass dominance. The "fluid" component of this habitat mosaic suggests compatibility between functional longleaf pine- bunchgrass systems and renewable resource use. Longleaf pine has been intensively exploited since colonial times. It is estimated that less than 3 million acres of the original 93 million and fewer than 1,000 acres of old-growth remain. As early as 1907, Munger (cited in Biswell 1989) warned that this ecosystem was rapidly disappearing. Yet even today attrition continues to take place at about 140,000 acres per year. Many intrinsic plants and animals are on the federal or various state lists of threatened and endangered species. Hardin and White (1989) believe extreme habitat reduction is the primary cause of the precarious state of over 191 taxa of vascular plants associated with the longleaf-wiregrass system.

Nevertheless, we recommend extraction of high-value products continue. Poles can bring 20 percent or more income than sawtimber, and longleaf produces more poles than other southern pines, 65 percent or more of the stems if managed properly (Farrar 1991). Properly conducted timber harvest mimics natural disturbance creating conditions favorable to the establishment of longleaf regeneration. Income from timber products can be augmented by hunting leases and judicious grazing (Wade and Lewis 1987).

If a complete system is to be maintained, however, use must not exceed the capacity of longleaf pine and bunchgrass to maintain their dominant role in the dynamic balance with normal disturbance. Beyond this point, resources can change abnormally, extrinsic competitors can invade, and intrinsic diversity can decline. Therefore, the degree to which ecological and economic systems can be jointly sustained is a matter of temporal-spatial scale of mosaics; the maintenance of groundcover patterns, multiple pine ages, and enough heartwood pines and snags for all native species to survive will be most difficult to coordinate with resource use.

Experimental research is needed to identify the limits to which the ecosystem can absorb wood extraction and associated site disruption. As Bird (1994) states, our challenge "is finding the right balance of action".

We envision the task of perpetuating this ecosystem will become increasingly difficult to achieve in the face of expanding federal, state and local regulations - some of which are in potential conflict such as the Clean Air Act and The Threatened and Endangered Species Act. Other critical issues that society will eventually have to decide include fire safety and smoke management considerations along the urban/wildland interface. Successful restoration of this ecosystem will require the concentrated region-wide commitment of federal and state agencies, and especially the private sector, all working in concert to remove existing disincentives, promote the economic and ecological value of longleaf pine, and facilitate its expansion throughout its historic range.

LITERATURE CITED

Abrahamson, Warren G. and David C. Hartnett, 1990. p. 103-149. In: Myers, R.L., and Ewel, J.J. editors. Ecosystems of Florida. University of Central Florida Press. Orlando, FL.

Bird, Joan 1994. Managing biodiversity. Nature Conservancy 44(1):22-27.

Boyer, W.D. 1990. Growing-season burns for control of hardwoods in longleaf pine stands. USDA Forest Service, Southern Forest Experiment Station, Research Paper SO-256. 7p.

Chapman, H.H. 1957. Forty-year effect of a summer fire on 4-year-old longleaf pine at Urania, Louisiana. Journal of Forestry 55(4):301-302.

Christensen, Norman L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the Coastal Plain of North Carolina. Oecologia 31:27-44.

Christensen, Norman L. 1981. Fire regimes in southeastern ecosystems. p. 112-136. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E., and Reiners, W.A. editors. Fire regimes and ecosystem properties. USDA Forest Service, Washington Office, General Technical Report WO-26.

Delcourt, Paul A. and Hazel R. Delcourt, 1987. Long-term forest dynamics of the temperate zone. Springer-Verlag, NY. 439p.

Farrar, Robert M. 1991. A new look at longleaf pine. The Consultant, fall:18-21.

Frost, C.C. Four centuries of changing landscape patterns in the longleaf pine ecosystems. Tall Timbers Fire Ecology Conference 18:(in press).

Gilliam, Frank S. 1988. Interactions of fire with nutrients in the herbaceous layer of a nutrient-poor Coastal Plain forest. Bulletin of the Torrey Botanical Club 115(4):265-271.

Hardin, E.D., and D.L. White, 1989. Rare vascular plant taxa associated with wiregrass (Aristida stricta) in the southeastern United States. Natural Areas Journal 9:234-245.

Hermann, S.M. Small-scale disturbance in an old-growth longleaf pine forest. Tall Timbers Fire Ecology Conference 18:(in press).

Heyward, F. and A.N. Tissot, 1936. Soil changes in the soil fauna associated with forest fires in the longleaf pine region. Ecology 17:659-666.

Hodgkins, E.J. 1958. Effects of fire on undergrowth vegetation in upland southern pine forests. Ecology 39:36-46.

Jackson,D.R. 1989. The fauna of gopher tortoise burrows. p. 86-98. In Diemer, J.E., D.R. Jackson, J.L. Landers, J.N. Layne, and D.A. Wood editors, Gopher Tortoise Relocation Symposium Proceedings Florida Game and Fresh Water Fish Commission Nongame Wildlife Program Technical Report 5.

Komarek, E.V. 1964. The natural history of lightning. Tall Timbers Fire Ecology Conference 3:139-183.

Komarek, E.V. 1968. Lightning and lightning fire as ecological forces. Tall Timbers Fire Ecology Conference 8:169-197.

Landers, J.L. 1991. Disturbance influences on pine traits in the southeastern United States. Tall Timbers Fire Ecology Conference 17:61-98.

Landers, J.L., N.A. Byrd, and R. Komarek, 1990. A holistic approach to managing longleaf pine communities. p. 135-167. In: Farrar, R.M. Jr. editor, Proceedings Symposium on the Management of Longleaf Pine, April 4-6, 1989, Long Beach, MS. General Technical Report SO-75. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA.

Lewis, C.E. and R.H. Hart, 1972. Some herbage responses to fire on pine-wiregrass range. Journal of Range Management 29:209-213.

McKee, W.H. 1982. Changes in soil fertility following prescribed burning on Coastal Plain pine sites. Research Paper SE-234. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC. 23p.

Munger, T.T. 1907. Cited (without complete citation on p. 83) in Biswell 1989. Prescribed burning in California wildlands vegetation management. University of California Press, Berkeley, CA. 255p.

Myers, Ronald L. 1990. Scrub and high pine. p. 150-193. In: Myers, R.L., and Ewel, J.J. editors. Ecosystems of Florida. University of Central Florida Press. Orlando, FL.

Neumann, C.J., G.W. Cry, E.L. Caso, and B.R. Jarvinen. 1981. Tropical cyclones of the North American Ocean, 1871-1980. USDC National Oceanic & Atmospheric Administration, National Climate Center, Asheville, NC. 174p.

Peet, R.K. and D.J. Allard. Longleaf pine-dominated vegetation of the southern Atlantic and eastern Gulf Coast region, USDA. Tall Timbers Fire Ecology Conference. 18:(in press).

Platt, W.J., G.W. Evans, and S.L. Rathbun, 1988. The population dynamics of a long-lived conifer (Pinus palustris). American Naturalist 131:491-525.

Plummer, G.L. R.M. Greenwald, and W.W. Davis, 1980. Climatic periods and trends in a rainshawdow ecosystem: interpretation of changes in Augusta, Georgia. Georgia Journal of Science 38:185-198.

Schwarz, G.F. 1907. The longleaf pine in virgin forest, John Wiley & Sons, New York. 134p.

Stout, I. Jack, and Wayne R. Marion, 1993. Pine flatwoods and xeric pine forests of the southern (lower) Coastal Plain. p. 373-446. In: Martin, W.H., Boyce, S.G., and Echternacht, A.C. editors. Biodiversity of the southeastern United States. John Wiley & Sons, New York.

Wade, Dale D. and Clifford E. Lewis, 1987. Managing southern grazing ecosystems with fire. Rangelands 9(3):115-119.

Watts, W.A. 1980. The late quaternary vegetation history of the southeastern United States. Annual Review of Ecology and Systematics 11:387-409.

Ware, Stewart, Cecil Frost and Phillip D. Doerr, 1993. Southern mixed hardwood forest: The former longleaf pine forest. p. 447-493. In: Martin, W.H., Boyce, S.G., and Echternacht, A.C. editors. Biodiversity of the southeastern United States. John Wiley & Sons, Incorporated. NY.

Weigl, P.D., M.A. Steele, L.J. Sherman, J.C. Ha, and T.C. Sharpe, 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: Implications for survival in the Southeast. *Tall Timbers* Research Station Bull. 24. 93p.